The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots

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The mechanisms underlying the taxonomic assembly of montane biotas are still poorly understood. Most hypotheses have assumed that the diversification of montane biotas is loosely coupled to Earth history and have emphasized instead the importance of multiple long-distance dispersal events and biotic interactions, particularly competition, for structuring the taxonomic composition and distribution of montane biotic elements. Here we use phylogenetic and biogeographic analyses of species in the parrot genus *Pionus* to demonstrate that standing diversity within montane lineages is directly attributable to events of Earth history. Phylogenetic relationships confirm three independent biogeographic disjunctions between montane lineages, on one hand, and lowland dry-forest/wet-forest lineages on the other. Temporal estimates of lineage diversification are consistent with the interpretation that the three lineages were transported passively to high elevations by mountain building, and that subsequent diversification within the Andes was driven primarily by Pleistocene climatic oscillations and their large-scale effects on habitat change. These results support a mechanistic link between diversification and Earth history and have general implications for explaining high altitudinal disjuncts and the origin of montane biotas.

Keywords: montane biotas; historical biogeography; speciation; diversification; Andes; Psittacidae

1. INTRODUCTION

Formed behind an eastward-dipping ocean–continental subduction zone, the Andes stretch more than 7000 km from Colombia to Chile and have extensive land area above 4000 m, particularly from Peru through northern Chile and Argentina. This topographic complexity, and the fact that the Andes border the megadiverse lowland Amazonian biota, has contributed to their harbouring the world's most diverse montane avifauna in terms of numbers of species as well as endemics (Fjeldså & Krabbe 1990; Stotz *et al.* 1996).

The origin of the montane Andean flora and fauna, and specifically that of birds, is poorly understood. Two general hypotheses have been proposed. The most widely invoked is that montane elements have been largely derived from lowland relatives via long-distance dispersal (Descimon 1986; Monasterio & Vuilleumier 1986; van der Hammen & Cleef 1986) or by colonization as populations expanded their ranges upslope, became isolated due to climatically induced habitat change, and then became differentiated (Brumfield & Edwards 2007). An alternative hypothesis is that ancestral populations were distributed across both lowland and pre-Andean landscapes, with tectonic uplift passively transporting some to increasingly higher elevations where they

differentiated within a variety of montane habitats (Lynch 1986; Reig 1986; van der Hammen & Cleef 1986; Hall 2005).

Neither hypothesis would be expected to be applicable across all groups, and it might not always be possible to distinguish between them in specific cases. What has generally been lacking in earlier studies, however, is a corroborated phylogenetic hypothesis, which, along with inferences about the spatial and temporal history of the group, could be used to discriminate between these two alternatives. Following vicariance biogeographic principles (Nelson & Platnick 1981), Lynch (1986) outlined such a test, applied it to several small clades of frogs in the genus *Eleutherodactylus*, and proposed that lowland/montane disjunctions were the result of vicariance. Later, Bates & Zink (1994) implied altitudinal vicariance for four species of tyrannid flycatchers (*Leptopogon*). Using a general mitochondrial clock calibration of 2% divergence per million years (Myr), they estimated a lowland/montane age of vicariance at 9–6 Myr (ago). Recently, Hall (2005) constructed a phylogeny for 11 species of butterflies (*Ithomiola*), and inferred a vicariance origin for the montane taxa, but did not provide a temporal framework.

Here we describe the phylogenetic and biogeographic history of species within a single monophyletic genus of parrots (*Pionus*) and infer three independent instances of lowland/high montane vicariance and subsequent diversification. We use phylogenetic and biogeographic patterns,

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as well as multiple estimates of divergence times based on molecular sequence data, to propose a causal link between diversification and Earth history, including mountain building and climatic oscillations, as understood from tectonic, palaeogeographic and palaeobotanical data. We discuss the implications these results have for investigating the origins of montane biotas and for understanding mechanisms of biological diversification.

2. MATERIAL AND METHODS

(a) *Taxonomic diversity and phylogenetic species*

Discovery of all smallest diagnosable taxonomic units, or phylogenetic species, is critical for describing how a group's taxonomic diversity originated across space and time (Cracraft 1997). Our starting point was to test whether previously described subspecies of *Pionus* are diagnosably distinct (phylogenetic species); therefore, we scored 18 external morphological characters for all subspecies (Forshaw 1989; Juniper & Parr 1998) using a large series of museum study skins (498 individuals; see table S1 and 'Taxonomic diversity and distributions', both in the electronic supplementary material).

(b) *DNA sequence acquisition*

We collected different sets of molecular data. For reconstructing species-level phylogenetic relationships, we obtained 2181 base pairs (bp) of sequence for the complete cytochrome *b* (*cyt b*, GenBank accession numbers EF517602–EF517636) and NADH dehydrogenase 2 (*ND2*, GenBank accession numbers EF517637–EF517671) mitochondrial genes from 35 individuals representing all 19 presumptive phylogenetic species within *Pionus* (table S2 in the electronic supplementary material). Monophyly of *Pionus* was confirmed by undertaking preliminary analyses using a diversity of South American parrots with presumed close and distant relationships (Tavares *et al.* 2004, 2006; Ribas *et al.* 2005; for further details see 'methods' in the electronic supplementary material). From these analyses, close relatives of *Pionus*, including *Gypopsitta barrabandi*, *Amazona farinosa*, *Amazona xanthops* and *Graydidascalus brachyurus*, were chosen as outgroups.

For the molecular clock analyses, sequences from the nuclear recombination activating genes, *RAG-1* and *RAG-2*, were obtained for several genera of parrots (table S3 in the electronic supplementary material). Most *RAG-1* sequences were obtained from GenBank from a recent study (Tavares *et al.* 2006) that focused on Neotropical genera. *RAG-2* sequences were obtained in our laboratory for selected genera including all main lineages of parrots, all main Neotropical lineages, and five *Pionus* species (table S3).

(c) *DNA extraction, sequencing and phylogenetic data analysis*

DNA extraction, amplification, sequencing and alignment were performed as described (Ribas *et al.* 2005, 2006; for further details see 'methods' in the electronic supplementary material). All primers used are shown in table S4 (in the electronic supplementary material).

Tests were performed to assess incongruence of phylogenetic signal between the two mitochondrial genes and among all three codon positions (ILD test; Farris *et al.* 1995). We further determined whether there was evidence of saturation due to multiple substitutions and evaluated the uniformity of base composition (see 'methods' in the electronic supplementary material).

Phylogenetic hypotheses were constructed through heuristic maximum-parsimony (MP) and maximum-likelihood (ML) searches in PAUP* v. 4.0b10 (Swofford 2002), as well as with Bayesian analysis using MrBayes v. 3.1 (Huelsenbeck & Ronquist 2001). For MP analyses of the combined morphological and molecular data, the 18 morphological characters were added to a molecular matrix containing only one representative of each taxon. Support for nodes in MP and ML was assessed using the non-parametric bootstrap. Bayesian analyses were conducted with a mixed-model approach. Three independent analyses of 10 million generations each were performed (for further details on MP, ML and Bayesian analyses see 'methods' in the electronic supplementary material).

(d) *Biogeographic analyses*

Because montane versus lowland elevational distributions are discrete, they were scored as a binary character and each species was coded as being either lowland or montane (distributional data are provided in 'taxonomic diversity and distributions' in the electronic supplementary material). Historical biogeographic change in elevational distribution was assessed using ancestral character-state reconstruction with delayed optimization (Maddison & Maddison 1999).

(e) *Molecular dating of divergence times*

Estimating ages of divergence across lineages with precision is subject to many caveats (Arbogast *et al.* 2002; Lovette 2004), thus our goal was to seek an internally consistent estimate of divergence times. Because no fossil calibration exists for *Pionus*, three different strategies were implemented to test for consilience in age estimates.

Our first approach employed rates of molecular evolution in *cyt b* to bracket divergence time estimates in *Pionus*. The most commonly used rates for *cyt b* have been 1.6% (Fleischer *et al.* 1998) and 2% (Brown *et al.* 1979; Randi 1996) sequence divergence per million years (Myr). It is not known how applicable these rates are across birds as a whole, but the congruence of rates estimated from different studies lends some credibility to using them to bracket divergence times in groups for which no fossil record is available. As *Pionus cyt b* sequences evolve in a clock-like manner ($p > 0.1$, likelihood ratio test), we adopted both 1.6 and 2% rates to convert ML distances to times of divergence within *Pionus*.

For the remaining two strategies, relaxed molecular clock methods were employed. Penalized likelihood (PL) allows for different rates of evolution across the tree, but applies a non-parametric roughness penalty (rate smoothing) that costs the model more if rates change too quickly between branches (Sanderson 2002). The parametric method proposed by Thorne *et al.* (1998) uses a probabilistic model based on priors to describe the change in evolutionary rates over time and uses the Markov chain Monte Carlo procedure to derive the posterior distribution of rates and times.

Previous phylogenetic studies have shown that the endemic New Zealand parrot genera, *Nestor* and *Strigops*, are basal to all other parrots (de Kloet & de Kloet 2005; Tavares *et al.* 2006). This provides a framework for calibrating this basal split using the date of geological separation of New Zealand from West Antarctica (e.g. Barker *et al.* 2004; Tavares *et al.* 2006), estimated to be 85–82 Myr ago (Yan & Kroenke 1993). Because saturation of nucleotide substitutions places limits on the use of mtDNA sequences for dating deep phylogenetic nodes (Jansa *et al.* 2006; Roelants *et al.* 2007), we employed
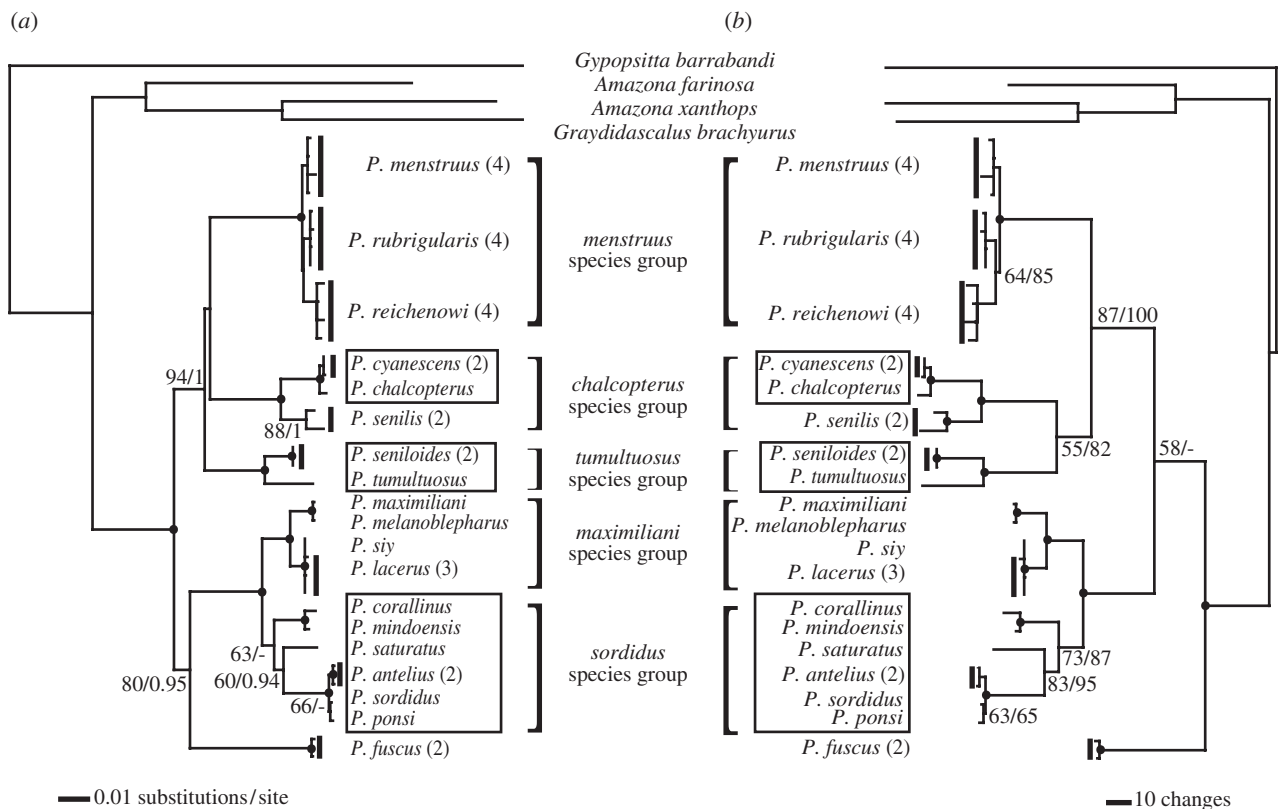
(a)

(b)

Gypopsitta barrabandi
Amazona farinosa
Amazona xanthops
Graydidascalus brachyurus

Figure 1. Topologies generated by the combined analysis of cyt *b* and ND2 (2181 bp). Numbers in parenthesis indicate the number of specimens sampled. Boxes highlight the tree montane clades. (*a*) ML topology using the GTR+Γ model. Numbers along branches indicate ML bootstrap values greater than 50%/Bayesian posterior probabilities greater than 0.9. Solid circles indicate a bootstrap value greater than 95% and a posterior probability of 1.0. (*b*) MP topology. Numbers along branches are MP bootstrap values greater than 50% without/with the morphological characters included in the analysis. Solid circles indicate a bootstrap value greater than 95%.

nuclear sequences to estimate divergence dates across a generic tree for parrots using the New Zealand geological calibration. We then adopted these dates to calibrate the mtDNA tree for *Pionus* (see Wiens *et al.* 2007). Thus, we built a tree for *RAG-2* sequences (1155 bp, GenBank accession numbers EF517676–EF517702) for 22 genera of parrots, including 5 *Pionus* species (table S3) and analysed their temporal diversification with both r8s (PL, Sanderson 2003) and MULTIDIVTIME (Thorne & Kishino 2002), fixing the age of the split between *Nestor* and all other genera at 85 Myr ago. Results from this analysis were then used to calibrate the mtDNA *Pionus* phylogeny (for details on the settings used for both r8s and MULTIDIVTIME analyses, see 'methods' in the electronic supplementary material).

Our final approach was designed to examine the precision of the ages determined by *RAG-2*. We obtained nuclear *RAG-1* (2703 bp) sequences from GenBank (Tavares *et al.* 2006) for 30 parrot genera. As this pre-existing dataset was composed mostly of Neotropical genera, we added *RAG-1* sequences from *Nestor notabilis*, *Agapornis personata*, *Micropsitta bruijnii* and *Psittacus erithacus* (table S3; GenBank accession numbers EF517672–EF517675), so that the same geological calibration could be applied. The final *RAG-1* matrix had 34 terminals, including 14 genera in common with the *RAG-2* dataset.

3. RESULTS
(a) *Basal taxa (phylogenetic species)*
Morphological and genetic data support the recognition of 19 phylogenetic species, although additional sampling will

be required to corroborate the status of several of these taxa (for details, see 'Taxonomic diversity and distributions' in the electronic supplementary material).

(b) *Phylogenetic analyses*
No insertions or deletions were found, and start and stop codons were in the expected positions. Patterns of base composition were as expected for avian mtDNA. No base composition bias was detected ($p=0.08$ for *cyt b* and $p=0.95$ for *ND2*). The incongruence length difference test (ILD; Farris *et al.* 1995) rejected incongruence between the two genes ($p>0.05$) and among the three codon positions (*cyt b* $p>0.15$ and *ND2* $p>0.20$). Plots of pairwise divergences (Ts and Tv versus *p*-distance) did not show evidence of saturation. The GTR +Γ model was implemented for cyt *b* ($\alpha=0.155$) and combined ($\alpha=0.195$) mitochondrial data, while TrN+Γ was applied to the *ND2* ($\alpha=0.238$) data.

The trees found by ML and MP analyses are shown in figure 1. Bayesian analysis yielded the same topology as the ML tree. Five clades (species groups) were recovered, four of which (*menstruus*, *chalcopterus*, *tumultuosus* and *maximiliani*) have strong support. The *sordidus* species group was less well supported but was monophyletic in all analyses, especially when morphological characters were added to the molecular data (figure 1*b*). There was consistently high support for a relationship between the *menstruus*, *chalcopterus* and *tumultuosus* species groups, on one hand, and the *maximiliani* and *sordidus* groups on the other, but two phylogenetic uncertainties were also
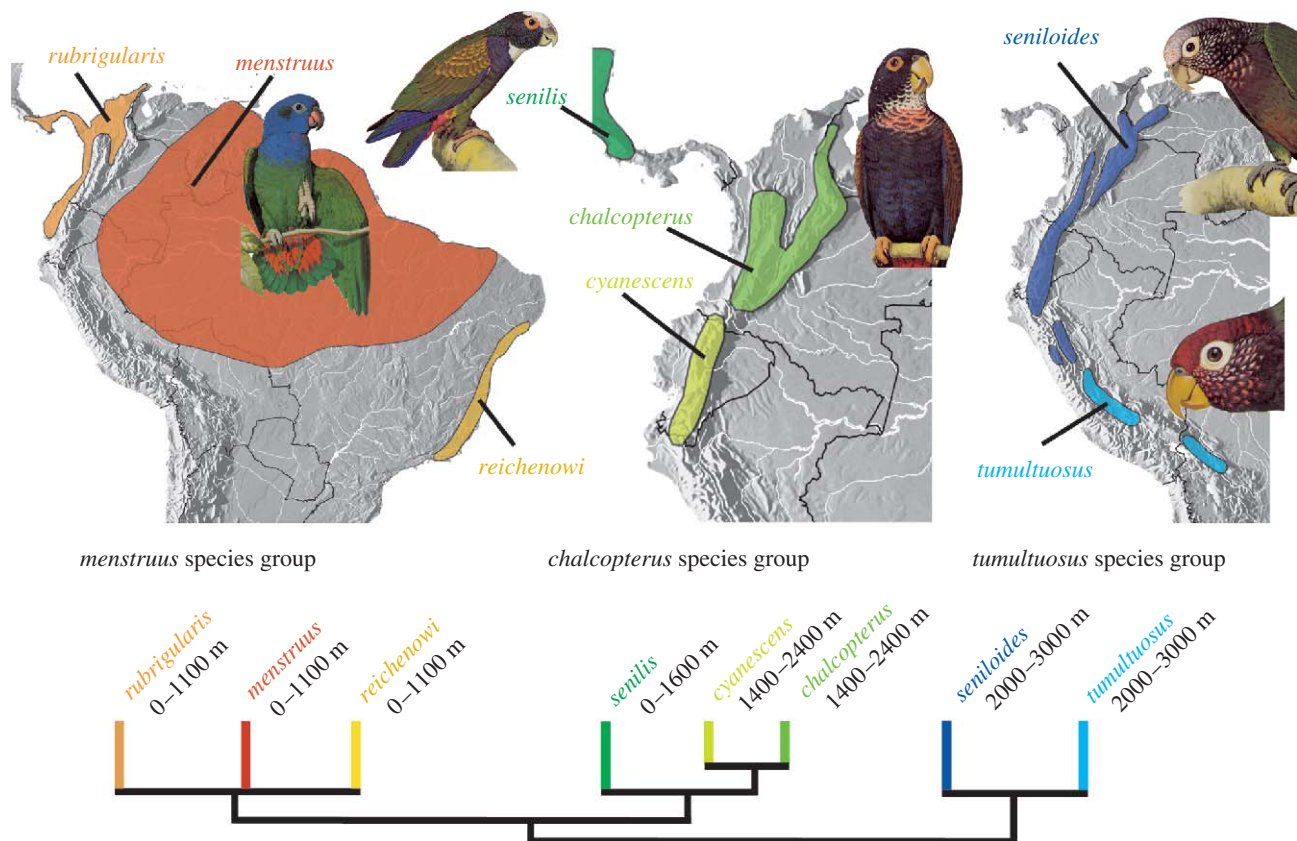
Figure 2. Distribution and altitudinal ranges of the *menstruus*, *chalcopterus* and *tumultuosus* species groups. Phylogenetic relationships are based on ML analysis (figure 1*a*). See electronic supplementary material for detailed discussion about distributions and altitudinal ranges. Plates courtesy of William T. Cooper (*Parrots of the world*, 1st edn, 1973).

revealed. First, both ML and Bayesian analyses united the *menstruus* and *chalcopterus* groups with low support (figure 1*a*), whereas MP clustered the *chalcopterus* and *tumultuosus* groups. This latter clade had low MP support with molecular data alone but had moderate support when morphological characters were included (figure 1*b*). Second, *Pionus fuscus* is an old lineage, and its association with the *maximiliani* + *sordidus* clade appeared in ML and Bayesian analyses with high support. In contrast, the MP analysis placed *P. fuscus* basal to all other *Pionus* taxa, but this arrangement had very low support (figure 1*b*).

(c) *Biogeographic patterns within* Pionus
Phylogenetic results revealed that the three Andean clades are not jointly monophyletic but instead have independent relationships to lowland taxa (figure 1). *Pionus chalcopterus* and *Pionus cyanescens* are mid-montane sister taxa of the northern Andes (figure 2). Together they are related to *P. senilis*, a lowland species of Middle America and Mexico. On the ML tree, these three species are related to the lowland *menstruus* species group, which exhibits classic *cis*-, *trans*-Andean and Brazilian Serra do Mar tropical forest distributions. The sister group of these two species groups, as determined by ML, is the *tumultuosus* species group. The latter contains two high montane species, *Pionus tumultuosus* and *Pionus seniloides*. The MP solution (figure 1*b*) united the *chalcopterus* and *tumultuosus* species groups, and thus on the MP tree montane origins are optimized ambiguously: either there was a single origin for the *chalcopterus* and *tumultuosus* species groups, with a reversal back to lowlands in *Pionus senilis*, or these

species groups became montane independently. Divergence time estimates, discussed below, suggest *P. senilis* separated from *P. cyanescens/P. chalcopterus* 2.2–1.2 Myr ago (table 1, node 5), after the emplacement of continuous Panamanian Isthmus lowlands (Duque-Caro 1990). This finding, and the fact that the current distribution of *P. senilis* is centred in the lowlands, strongly implies a primitively lowland distribution for this species. Both trees of figure 1 thus point to three independent montane origins.

Nearly all species of *Pionus*, particularly the montane ones, have their distributions in one or more long-recognized areas of endemism (Cracraft 1985*a*). Shared patterns of endemism are most parsimoniously explained in terms of a common vicariance history (Nelson & Platnick 1981; Cracraft 1992, 1994), and indeed sister species within montane *Pionus* are allopatric, so that their distributions are consistent with vicariance. Species ranges within *Pionus* are limited by many of the same barriers that affect other montane groups, primarily strong topographical lows having disparate ecologies (e.g. hotter lowland forest or drier intermontane shrubland) when compared with adjacent montane forests.

Examining distributions of Andean species groups phylogenetically reveals shared montane ecological histories within, but disparity among, these clades (figures 2 and 3). Of the three montane clades, the two species of the *tumultuosus* species group occur at the highest elevations in the high temperate zone and both range between 2000 and 3000 m (figure 2). Intermediate in altitude are the highland species within the *chalcopterus* species group (figure 2), with both species being found in mid-montane cloud forests. Finally, taxa of the *sordidus*

Table 1. Estimates of divergence time (Myr ago) within *Pionus*. Nodes are numbered as in figure 4. Fixed calibration times marked with asterisks are derived from a *RAG-2* analysis as described in §2 (see also electronic supplementary material, table S5).

| | cytochrome *b* | | cytochrome *b*+*ND2* | | cytochrome *b*+*ND2* | |
| | 1.6% | 2.0% | penalized likelihood (*r8s*) | | Bayesian (MULTIDIVTIME) | |
node			mean	95% interval	mean	95% interval
1	—	—	9.21*	—	13.30*	—
2	5.83	4.66	4.28*	—	6.90*	—
3	4.38	3.50	3.36	2.08–4.71	5.58	4.46–6.69
4	0.43	0.34	0.37	0.15–0.63	0.76	0.33–1.41
5	1.93	1.54	1.22	0.78–1.74	2.18	1.27–3.30
6	0.25	0.20	0.19	0.12–0.45	0.45	0.12–0.92
7	1.50	1.20	1.29	0.75–1.91	2.34	1.41–3.50
8	5.00	4.00	3.81	2.04–5.14	6.31	5.30–6.91
9	2.38	1.90	1.68	1.26–2.16	2.98	1.98–4.18
10	1.15	0.92	0.64	0.38–0.98	1.18	0.53–2.06
11	0.06	0.05	0.04	0.00–0.15	0.15	0.01–0.45
12	0.04	0.03	0.02	0.00–0.11	0.12	0.01–0.35
13	1.94	1.55	1.35	0.95–1.83	2.41	1.52–3.50
14	0.66	0.53	0.23	0.005–0.49	0.34	0.02–0.91
15	1.66	1.33	1.14	0.84–1.54	2.01	1.18–3.02
16	0.25	0.20	0.11	0.00–0.27	0.32	0.06–0.73

species group have the lowest altitudinal distributions of the three montane clades and occupy low- to mid-montane forests and may range to lower elevations, especially in northern Venezuela (figure 3; for further details about distributions, see 'taxonomic diversity and distributions' in the electronic supplementary material).

(d) *Temporal pattern of diversification.*
Based on age estimates using rates of 2.0 and 1.6% sequence divergence per Myr, the basal split within *Pionus* (figure 4, node 2) took place between *ca* 4.7 Myr ago and a maximum of *ca* 5.8 Myr ago (table 1). Importantly, the estimated dates bracket the origins of the three montane lineages as having taken place between *ca* 4.4 and 1.5 Myr ago (table 1, nodes 3, 5 and 9) and also suggest that the radiation of extant species was almost entirely within the Pleistocene.

MP and ML analyses of the *RAG-2* dataset resulted in a topology that agrees with previously inferred phylogenetic relationships among parrot genera (de Kloet & de Kloet 2005; Tavares *et al.* 2006), with the species of *Pionus* forming a well-supported clade, and the New Zealand genus *Nestor* resolved as the sister group of all other parrots (figure S1 in the electronic supplementary material). A PL analysis of the *RAG-2* ML tree, using the external geological calibration, estimated the split between *Pionus* and its sister genera, *Graydidascalus* and *Amazona*, at *ca* 9.2 Myr ago (95% CI: 3.9–18.5 Myr ago), whereas the most basal split within *Pionus* took place *ca* 4.3 Myr ago (95% CI: 1.2–12.4 Myr ago; nodes 8 and 9; table S5 in the electronic supplementary material). The Bayesian analysis of the same *RAG-2* data estimated these two splits at *ca* 13.3 Myr ago (95% CI: 5.2–26 Myr ago and 6.9 Myr ago (95% CI: 1.7–16 Myr ago), respectively (nodes 8 and 9, table S5).

Splits inside *Pionus* were estimated using the mtDNA dataset and applying the *RAG-2* dates as calibration points. Excluding the most basal (fixed-age) node, divergence dates within *Pionus* ranged from 3.81 to
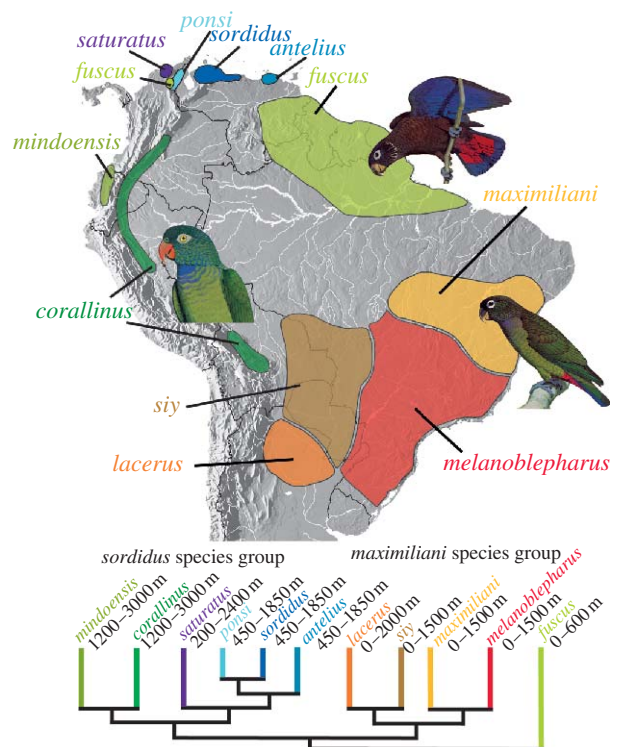

Figure 3. Distribution and altitudinal ranges of the *sordidus* and *maximiliani* species groups and *P. fuscus*. Phylogenetic relationships are based on ML analysis (figure 1a). See electronic supplementary material for detailed discussion about distributions and altitudinal ranges. Plates courtesy of William T. Cooper (*Parrots of the world*, 1st edn. 1973).

0.02 Myr ago using PL and from 6.31 to 0.12 Myr ago in the Bayesian analysis. The dates and confidence intervals are given in table 1, and the chronogram derived from the Bayesian analysis is shown in figure 4.

PL and Bayesian analyses of the *RAG-1* dataset using the same settings and calibration point as that for *RAG-2* resulted in the dates and confidence intervals shown in table S5.
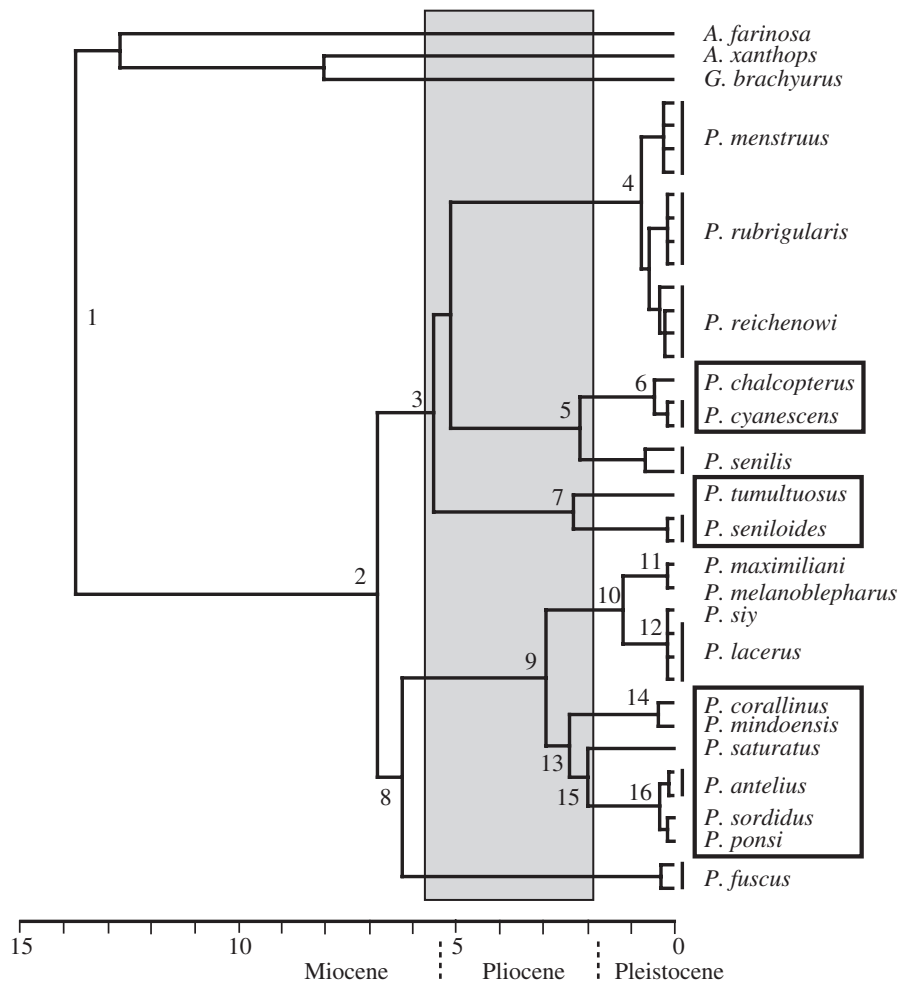
Figure 4. Bayesian MULTIDIVTIME chronogram based on the combined *ND2* and *cyt b* datasets. Nodes 1 and 2 are fixed calibration points derived from a Bayesian MULTIDIVTIME analysis of *RAG-2* data. Time scale is in millions of years. Numbered nodes correspond to those of table 1. Montane clades are shown in boxes. Shaded area shows estimated window of time during which montane/lowland vicariance occurred.

Despite disparate taxon sampling between the *RAG-1* and *RAG-2* datasets, estimated ages for the nodes common to both analyses were similar (figures S1 and S2, and table S5), strengthening our calibration of the mtDNA *Pionus* tree.

We found slight biases related to the different datasets and method of analysis. *RAG-1* age estimates are slightly older than *RAG-2* using the same geological calibration point and same methods, and Bayesian estimates are older than those for PL, given the same calibration and data. As a result of this, the mtDNA age estimates within the genus are slightly younger using PL (table 1). Owing to the lack of multiple calibration points, confidence and credibility intervals are large and overlap substantially.

Despite the variance just noted, multiple approaches to dating diversification within *Pionus* yielded a consistent interpretation: (i) major lineages within the genus arose in the Late Miocene or Pliocene and (ii) most of the species arose in the Pleistocene (figure 4).

4. DISCUSSION

(a) *Vicariance origin of montane* Pionus *and Earth history*

Taken as a whole, several lines of evidence are consistent with a vicariance hypothesis for the origin of the three montane clades within *Pionus*. First, distributions of these clades are strongly allopatric relative to their lowland sister

clades, and in each case the putative barrier is intervening low montane forest or lowland moist or dry habitats created as the Andes uplifted. These highland/lowland disjunctions are therefore better explained by vicariance rather than three independent long-distance dispersal events. Second, within each montane clade, species are distributed allopatrically in well-known areas of endemism that are shared by many other montane clades of birds. Such congruent patterns of endemism imply a vicariant history in generating species diversity within those clades (Cracraft 1994). Finally, the reconstructed temporal history of diversification (figure 4) is correlative with the uplift history of the Andes, thus establishing a plausible causal linkage to the process of vicariance.

The Central Andean Altiplano and Eastern Cordillera of Peru and northern Bolivia had attained approximately 40–50% of its current elevation by 10 Myr ago, and 2300–3500 m additional uplift has taken place since then (Gregory-Wodzicki 2000). Palaeofloras (Gregory-Wodzicki *et al.* 1998; Gregory-Wodzicki 2000, 2002; Graham *et al.* 2001) and geological analyses (Barke & Lamb 2006; Ghosh *et al.* 2006) for the Eastern Cordillera of the Central Andes indicate Miocene–Pliocene (*ca* 6–5 Myr ago) palaeoaltitudes of approximately 1000–2000 m, which is much lower than present-day elevations (3500 m or greater). At that time, our data suggest that several lineages of *Pionus* were diversifying in this region (figure 4). A 1000–2000 m

palaeoaltitude is at the lower part of the current altitudinal range of one of these lineages, the *P. tumultuosus* species group, which is also the oldest montane clade. The habitat at 1000–1500 m would have been near the cloud forest/tropical forest interface (Graham *et al.* 2001). We estimate that between 5.58 and 2.34 Myr ago (nodes 3 and 7, table 1 and figure 4) the ancestor of *P. tumultuosus/ P. seniloides* would have been uplifted approximately 650–1000 m (at 0.2–0.3 mm/yr assuming continuous uplift; Gregory- Wodzicki 2000) and an additional 450–700 m since then, thereby transporting the lineage and its habitat from a subtropical/tropical zone to a temperate one.

In the northern Andes of Ecuador and Colombia, in contrast, the *chalcopterus* species group arose later in time (2.18 Myr ago; node 5, figure 4) and is distributed at lower elevations (figure 2), which may reflect differences in tectonic history. The Ecuadorian Cordillera began developing in the Middle Miocene, with uplift of approximately 6100 m taking place over Plio–Pleistocene times (Steinmann *et al.* 1999; Coltorti & Ollier 2000). The Eastern Cordillera of Colombia was a continuous range by 11.8 Myr ago (Hoorn *et al.* 1995; Flynn *et al.* 1997; Guerrero 1997), but at an elevation of approxi- mately 700 m it had lowland, or perhaps lower montane, forest depending on location (Gregory-Wodzicki 2000). The Eastern Cordillera of Colombia and the Merida Andes of Venezuela experienced rapid Plio–Pleistocene uplift (Gregory-Wodzicki 2000; Chacín *et al.* 2005), and montane forest environments were established via 1500–1800 m of uplift within the past 4 Myr (Gregory- Wodzicki 2000). This time frame of uplift is consistent with the origins of the *P. chalcopterus/cyanescens* clade (node 5, figure 4) and the *P. sordidus* species group (node 9, figure 4). Within the later, the first split (node 13, figure 4) isolated northern Colombian/Venezuelan taxa (*saturatus, antelius, sordidus* and *ponsi*) from the Central and Northern Andean taxa (*corallinus* and *mindoensis*) that occur today at higher elevations. This split is dated at *ca* 2.4 Myr ago, a time when the Northern Andes were undergoing their most recent significant burst of uplift. The northern Colombian/Venezuelan clade was isolated in the Mérida, Perijá and Santa Marta ranges and diversified during a period of uplift (Cediel *et al.* 2003), with the Santa Marta endemic (*Pionus saturatus*) being the first to be isolated at *ca* 2 Myr ago (node 15, figure 4). Finally, our temporal estimates (figure 4; table 1) suggest that *P. senilis* separated from *chalcopterus/cyanescens ca* 2.2 Myr ago, well after the Panamanian Isthmus was formed (Duque-Caro 1990). What isolated *senilis* and why it is not found in southern Panama are unknown.

(b) *Speciation and Pleistocene climate change*
Except for *P. tumultuosus, P. seniloides* and *P. saturatus*, all montane species apparently originated within the last 0.5 Myr (table 1). Distributional patterns and relationships of the latter are consistent with vicariance driven by cyclic climatic changes that shifted montane environments to lower elevations during cooler/drier (glacial) times and back to higher elevations during warmer/wetter (interglacial) periods (Haffer 1974). The elevation of the upper forest line has been estimated to have oscillated between 2000 and 3400 m in the Colombian Andes (Hooghiemstra & van der Hammen 2004; Weng *et al.* 2007). During interglacial conditions montane populations of *Pionus* would have been

isolated by intermontane valleys, tropical forest habitats or both. This mechanism has also been suggested to have promoted diversification in several other groups of Andean birds (Roy *et al.* 1997; García-Moreno *et al.* 1999*a,b*; Chesser 2000).

(c) *Vicariance, origin and evolution of montane avifaunas*
Although some phylogenetic studies of Andean birds have suggested that montane clades originated prior to the Pleistocene (Bates & Zink 1994; Bleiweiss 1998; Garcia- Moreno *et al.* 1998, 2001; Burns & Naoki 2004; Chesser 2004; Pérez-Emán 2005), the origins of those clades were not explicitly attributed to vicariance via Andean uplift (Bates & Zink (1994) and Bleiweiss (1998) implied a role for Andean uplift in establishing montane groups). Many authors, in contrast, have proposed that subsequent diversification within these groups was strongly influenced by tectonic activity and climate change (Garcia-Moreno *et al.* 1998, 2001; Pérez-Emán 2005; Cadena *et al.* in press; Chaves *et al.* 2007; among others). Thus, Andean orogenesis has been invoked more frequently as being important for generating diversity within the Andes rather than as a mechanism underlying the origin of the montane avifauna.

We propose that highland–lowland vicariance has been underappreciated for several reasons: (i) the relevant phylogenetic–biogeographic patterns have been over- looked, (ii) avian divergences are generally thought to be too young relative to the time scale of mountain building, (iii) it has long been assumed that ecological (biotic) factors structure altitudinal distributions, (iv) a vicariance split between disjunct montane and tropical lowland clades has been seen as improbable, and (v) some biogeographic methods, especially those that estimate ancestral nodal distributions across a tree using either a parsimony or model-based framework, can themselves create a bias for accepting a dispersalist interpretation. In contrast to Bates & Zink (1994) and this paper, other researchers have identified biogeographic disjunctions between highland and lowland sister groups but did not link their divergence to vicariance via mountain building, for example in *Henicorhina* wood-wrens (Dingle *et al.* 2006) and *Thamnophilus* antshrikes (Brumfield & Edwards 2007). The latter authors propose a 'coloniza- tion' model for some highland taxa, which they proposed post-dated Andean uplift, in contrast to the history suggested here for *Pionus*. Moreover, they applied their model to taxa that have large overlaps in altitudinal distribution, which further suggests it is not applicable to biogeographic patterns such as discussed here.

These observations lead to the conclusion that more attention should be paid to deciphering the phylogenetic and biogeographic histories of montane biotas. In addition to the Andes, mountain ranges in Eurasia, New Guinea and New Zealand underwent rapid elevational change in the Late Neogene; thus, it can be predicted that patterns of lowland/montane vicariance are likely to be more widespread than previously realized. This prediction is testable by biogeographic analysis of montane clades and their lowland sister groups. Many biogeographic studies of montane taxa do not include sampling of lowland relatives, thus lowland/highland vicariance has been probably overlooked. The approach discussed here can

also be used to test the hypothesis that mountain biotas are a source for tropical lowland diversity (Fjeldså 1994). Support for this hypothesis has lacked rigorous phylogenetic and historical biogeographic testing (but see Weir 2006), and our results provide a falsifying instance.

Finally, the observation that allopatric or parapatric distributions of congeners along an altitudinal gradient can be explained as a function of biotic interactions (Terborgh 1971; Diamond 1973) needs critical re-examination. Without discounting possible secondary effects of biotic interactions on distributions, our results and those of others (Arctander & Fjeldså 1994; Bates & Zink 1994; Garcia-Moreno *et al.* 1998, 1999*a*,*b*; Cadena 2007) demonstrate that altitudinally parapatric congeners are often not sister taxa, thus providing falsifying instances of the hypothesis of parapatric speciation across altitudinal zones. Increasingly, these studies suggest that allopatric speciation driven by Earth history can explain north–south and altitudinal distributional patterns and is likely to be the primary mechanism underlying the taxonomic assembly of montane communities.

(d) Drivers of diversification

Historical biogeographic analysis interpreted within a framework of Earth history (Nelson & Platnick 1981; Cracraft 1985*b*, 1992, 1994) is fundamental for developing a mechanistic understanding of biological diversification. Because speciation in plants and animals appears to be largely allopatric (Coyne & Orr 2004), historical biogeographic methods can be used to test the hypothesis (Cracraft 1992, 1994) that allopatry is predominately driven by vicariance due to geological/environmental change rather than by long-distance dispersal. This approach is essential for testing alternative hypotheses about the rate control of speciation, which, along with extinction, is the first-order determinant of patterns of diversity across space and time. The results of this study provide evidence that spatio-temporal diversification in *Pionus* is causally linked to Andean tectonic and palaeoclimate change through vicariance. Because many other species in the Andes share similar spatial patterns, it is probable that these physical controls on diversification extend to them as well.

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